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Population Modeling of Diamondback Terrapins

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Population Modeling of Diamondback Terrapins

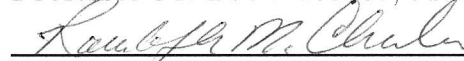
A thesis submitted in partial fulfillment of the requirement
for the degree of Bachelor of Science in Biology from
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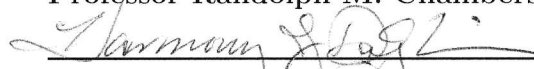
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Abstract

Diamondback terrapins are a species of turtle found along the coast of the United States from Massachusetts to Texas. Many of the states in this range list the terrapins as endangered, threatened, or a species of concern. However, little is known about their actual population sizes or dynamics. To address this, we use a nonlinear, stage-based model to examine the effects of human-related threats such as crab pots and road traffic. We compare our results to those produced by a linear model. When applied to a population of Rhode Island terrapins, our nonlinear model shows that crab potting has a larger negative effect on the population (which causes a population decline occurring at 6.6% mortality of affected stages) than road mortality (with a population decline at 10.6% mortality of affected stages). We also present population data gathered in the Williamsburg, VA area during the summer of 2013. We conclude that additional field work is needed in order to determine the status of many terrapin populations, but that in areas of existing crab potting, conservation efforts should focus on reducing terrapin mortality through the use of bycatch reduction devices.

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Chapter 1

Introduction



Figure 1.1: A seven year old male diamondback terrapin. Photo by Wendy Nelson (<http://vawendy.smugmug.com/Other/Terrapins>).

Diamondback terrapins are the only North American turtles that live exclusively in brackish water. They can be found along the east and gulf coasts of the United States from Cape Cod, Massachusetts to Corpus Christi, Texas. *Malaclemys terrapin terrapin* is the northernmost of seven subspecies and has a range extending from Massachusetts to North Carolina. The other subspecies are *centrata* (North Carolina to north Florida), *tequesta* (east coast of Florida), *rhizophorarum* (Florida Keys), *macrospilota* (west coast of Florida to the panhandle), *pileata* (Florida panhandle to Louisiana), and *littoralis* (Louisiana to Texas) [2].

There are conflicting reports as to how long a terrapin can live; some suggest the oldest terrapins are over 40 years old, while more conservative estimates fall

around 20 years [2]. We assume that 40 years is the maximum lifespan. Diamond-back terrapins feed on a variety of invertebrates including snails, clams, mussels, crabs, worms, and small fish [2]. They also incidentally consume a good deal of plant matter [23]. Adult terrapins are sexually dimorphic, with females obtaining a maximum plastron length of about 15 to 20 centimeters and males growing to roughly 10 to 13 centimeters. Females also have larger heads and shorter, thinner tails [2]. This sexual dimorphism may play a role in crab potting mortality (see Section 1.1) [18].

Breeding female terrapins lay anywhere from 10 to 30 eggs per year, depending on their age. The younger breeders lay one clutch of about 10 eggs, while the older breeders lay two to three clutches, each of about 10 eggs [1]. These breeders display strong nest site fidelity [4] and often make several trips onto land to scout out potential nesting sites before eventually laying their eggs [2].

Relatively little is known about the status of terrapin populations. Massachusetts and Rhode Island list terrapins as “threatened” and “endangered,” respectively. In states such as New Jersey and Virginia, however, they are listed as a “species of concern” due to a lack of adequate population data on which to base a status decision. Due to the number of threats of mortality in a terrapin’s environment [2], there is good reason to believe that the more relaxed listings should be amended.

1.1 Crab Potting and Road Mortality

Many terrapins are caught every year in crab pots. Attracted by the bait or curious about the pot, those terrapins that can fit enter the trap and drown when they are not able to find their way out. When one individual enters a pot, it becomes more likely that others will as well [2]. Hatchlings are small enough to swim out through the gaps in the traps, and adult females are too large to enter in the first place. Thus, juveniles of both sexes and adult males are disproportionately affected [18]. The threat to the population is exacerbated in the presence of “ghost pots,” which are abandoned, unbaited crab pots that still manage to attract and drown terrapins [2].

In 2007, Dorcas et al. examined the effects of crab potting on a population of terrapins in South Carolina. They used data gathered over a 21 year period and found that by the end of the period the population was smaller, had a higher proportion of older terrapins (most common age shifted from five to eight), and had significantly more females than males (from 45% to 80% female) [7].

Bycatch reduction devices (BRDs) can be attached to crab pots to exclude terrapins from the harvest. Developed by Roger Wood in 1992, these wire or plastic frames fit over the openings of the pots, reducing the size enough to prevent most



Figure 1.2: A blue crab caught in a crab pot. Photo by Wendy Nelson (<http://vawendy.smugmug.com/Other/Terrapins>).

terrapins from squeezing through while still allowing crabs to enter [2]. Although BRDs are quite effective at excluding terrapins, the catch of the target species in crab pots fitted with BRDs is variable by study and location. To date, four states (New York, New Jersey, Delaware, and Maryland) have regulations requiring the use of BRDs on crab pots [4].

Even though they cannot fit into crab pots, adult females are far from safe from human influences. Upon coming ashore to lay their eggs, terrapins may be run over by cars as they attempt to cross roads in search of a suitable nesting site [2]. A linear population model developed in [5] was used to show that road mortality had a definite negative effect on a population of Georgia terrapins. In this and other affected populations, some of the females killed by vehicles are attempting to lay their eggs right next to the road, while others are simply exploring the area as they look for an ideal nesting location [22]. The sandy beaches they once preferred may now lie under buildings and houses. Thus, some of the only lands left available to them are the grassy areas next to highways [24]. When females are killed by vehicles, the eggs can sometimes be salvaged from the remains of the mother and brought to term in a laboratory, but this requires timely action by an individual familiar with terrapin biology [2].

We will examine the effects of crab potting and road mortality on the long-term dynamics of a terrapin population. The results will demonstrate the levels of mortality at which the population reaches a tipping point between growth and decline. Based on the findings, we will suggest the types of conservation actions that can be taken in order to protect the population.

1.2 Classic Loggerhead Turtle Study

In 1987, Crouse et al. studied loggerhead sea turtles (*Caretta caretta*) using a stage-based population model. The female loggerheads were divided into seven stage classes based on similarities in life history traits: eggs/hatchlings, small juveniles, large juveniles, subadults, novice breeders, first-year remigrants, and mature breeders. A population matrix was constructed that included fecundity terms (the number of individuals produced per breeder per year), persistence terms (the fraction of a stage class that remains in that stage class from one year to the next), and growth terms (the fraction of a stage class that moves to the next stage class in a given year). This matrix was used to predict the future behavior of a theoretical loggerhead population, and to determine the sensitivity of the model to changes in the various parameters [6].

They found that the theoretical female population responded more drastically to changes in survival of juvenile and subadult stages than to increases in survival of the other stage classes, implying that conservation efforts ought to be focused on these intermediate stages [6]. This is not to say that nest site conservation efforts should be abandoned, but the same amount of effort directed towards the juvenile stage class, for instance, should yield better results.

Since the publication of Crouse's findings, conservation efforts aimed at loggerhead sea turtles have become much more prevalent. Turtle excluder devices (TEDs) are called for everywhere by federal regulations, and there are now signs on beaches educating visitors about how to avoid disturbing nesting loggerheads [14]. We use a model similar to that used by Crouse and colleagues [6] for a Rhode Island diamondback terrapin population, and hope that the results will contribute to conservation efforts as well.

Chapter 2

Model Development

2.1 Linear Model

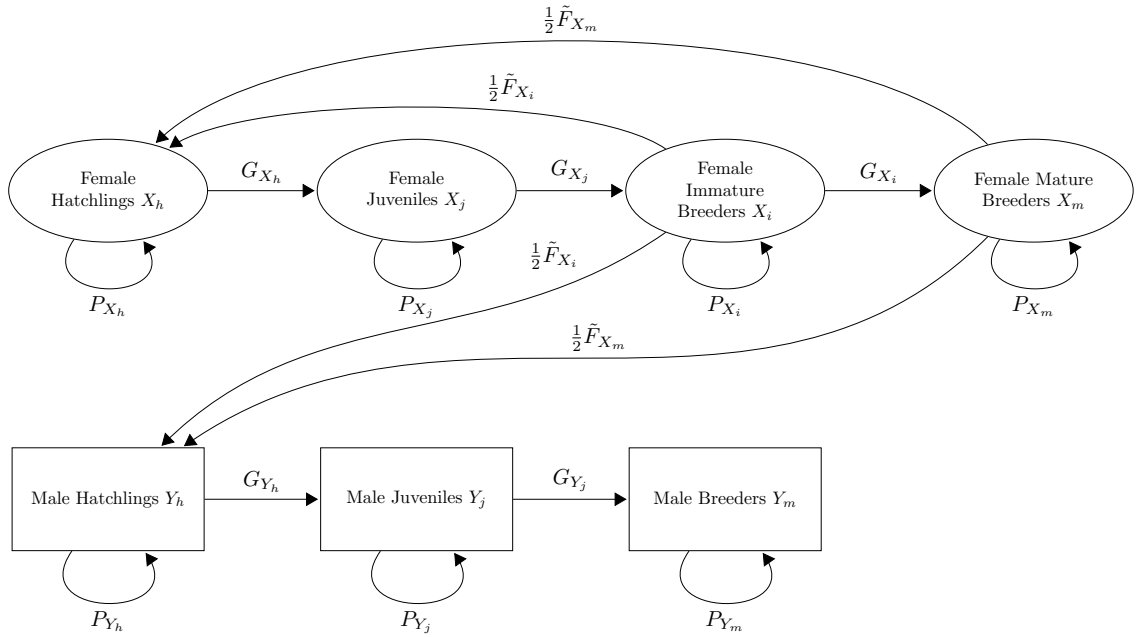


Figure 2.1: Life cycle graph for diamondback terrapins illustrating persistence (P), growth (G), and fecundity (\tilde{F}) (similar to [1]).

Matrix population models are an ideal way to examine the demography of populations whose members can be divided into stages. These stages can be made up of individuals of a range of ages who are assumed to have identical likelihoods of survival, growth, and reproduction. We consider two matrix models: a modified linear model from [1] and a nonlinear model. Unlike Crouse's paper [6], these models include the male stage classes. All data processing was performed in MATLAB

[12].

In the linear model, the terrapins are divided up into seven stage classes [1]: female hatchlings (X_h ; ages 1-2), female juveniles (X_j ; ages 3-7), immature female breeders (X_i ; ages 8-11), mature female breeders (X_m ; ages 12-40), male hatchlings (Y_h ; ages 1-2), male juveniles (Y_j ; ages 3-4), and male breeders (Y_m ; ages 5-40) (see Figure 2.1). The durations of the hatchling and juvenile stage classes were obtained from [13], and the age at first reproduction is corroborated by [19]. The immature and mature female breeders differ in the number of eggs they lay per year: 10 or 20 – 30, respectively (see Chapter 1) [1].

The rate of growth of a population (λ) and the probability of the survival of an individual in a certain stage class Z from year n to year $n + 1$ (σ_Z) can be determined based on data collected during field work. The growth parameter (γ_Z) is the probability of an individual developing to the next stage class if it is among those that will survive to the next year. This is given by

$$\gamma_Z = \frac{\left(\frac{\sigma_Z}{\lambda}\right)^{T_Z} - \left(\frac{\sigma_Z}{\lambda}\right)^{T_Z-1}}{\left(\frac{\sigma_Z}{\lambda}\right)^{T_Z} - 1} \quad (2.1)$$

[3], with T_Z the stage duration for each class, given by

$$T_Z = \begin{cases} 2, & Z = X_h, Y_h, Y_j \\ 5, & Z = X_j \\ 4, & Z = X_i \\ 29, & Z = X_m \\ 36, & Z = Y_m \end{cases}$$

[1]. For the mature stage classes X_m and Y_m , γ_Z corresponds to surpassing the maximum lifespan of 40 years.

Let $\vec{X}_n = [X_{h,n} \ X_{j,n} \ X_{i,n} \ X_{m,n} \ Y_{h,n} \ Y_{j,n} \ Y_{m,n}]^T$ (where T indicates that the matrix is transposed) be the vector of stage class abundances at year n . The linear model is given by $\vec{X}_{n+1} = A\vec{X}_n$, where

$$A = \begin{bmatrix} P_{X_h} & 0 & \frac{1}{2}\tilde{F}_{X_i} & \frac{1}{2}\tilde{F}_{X_m} & 0 & 0 & 0 \\ G_{X_h} & P_{X_j} & 0 & 0 & 0 & 0 & 0 \\ 0 & G_{X_j} & P_{X_i} & 0 & 0 & 0 & 0 \\ 0 & 0 & G_{X_i} & P_{X_m} & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2}\tilde{F}_{X_i} & \frac{1}{2}\tilde{F}_{X_m} & P_{Y_h} & 0 & 0 \\ 0 & 0 & 0 & 0 & G_{Y_h} & P_{Y_j} & 0 \\ 0 & 0 & 0 & 0 & 0 & G_{Y_j} & P_{Y_m} \end{bmatrix}. \quad (2.2)$$

Each of the persistence (P_Z) and growth (G_Z) parameters for stage class Z are

Parameter	Description
λ	Population growth rate
σ_Z	Probability of survival
σ_e	Probability of egg not being preyed upon
h	Probability of hatching of surviving eggs
γ_Z	Probability of surviving individual progressing to next stage class
P_Z	Rate of persistance in a stage class
G_Z	Rate of growth from one stage class to the next
F_{X_i}, F_{X_m}	Number of eggs per breeding female
$\tilde{F}_{X_i}, \tilde{F}_{X_m}$	Number of hatchlings that survive to year 1
u_i, u_m	Clutches per year per breeding female
k	Number of eggs per clutch
l	Longevity

Table 2.1: Table of parameters used for the linear and nonlinear models.

given by

$$\begin{aligned} P_Z &= \text{Prob}[\text{survive and not advance}] &= \sigma_Z(1 - \gamma_Z), \\ G_Z &= \text{Prob}[\text{survive and advance}] &= \sigma_Z\gamma_Z. \end{aligned} \quad (2.3)$$

The “fecundity” terms \tilde{F}_{X_i} and \tilde{F}_{X_m} give the number of hatchlings that survive to year 1,

$$\begin{aligned} \tilde{F}_{X_i} &= F_{X_i} h \sigma_e \sigma_h^{(3/4)}, \\ \tilde{F}_{X_m} &= F_{X_m} h \sigma_e \sigma_h^{(3/4)}, \end{aligned} \quad (2.4)$$

where $\sigma_h = \sigma_{X_h} = \sigma_{Y_h}$ and the $3/4$ corresponds to a 3 month incubation period, so that the hatchlings must survive for $3/4$ of the remaining year. The number of eggs per immature and mature female are given by $F_{X_i} = ku_i$ and $F_{X_m} = ku_m$, respectively. These and the other parameters are described in Table 2.1.

The population growth rate, λ , is the dominant eigenvalue of the matrix of parameters. So, it is the solution to $\det(A - \lambda I) = 0$, where I is the identity matrix. Multiple solutions are often possible, but the one we are concerned with is the dominant, or largest, eigenvalue. $\lambda > 1$ indicates that the population is growing, $\lambda < 1$ indicates it’s declining, and $\lambda = 1$ means that the population size is constant from one year to the next. Each eigenvalue is associated with an eigenvector, v , such that $Av = \lambda v$. The eigenvector associated with the maximal eigenvalue is the stable stage distribution of a population [3].

2.2 Nonlinear Model

The nonlinear model uses the same stage classes and parameters as the linear model with the exception of the fecundity terms, which are now frequency dependent and take into account the male contribution to fecundity. Male terrapins face different pressures than the females, and it is not reasonable to assume that the behavior of the female portion of the population accurately represents the trends in the male portion, especially considering the skewed effects of crab potting and road mortality [18] [2].

The frequency dependent nature of the fecundity terms implies that the number of eggs laid in a given year depends not on the absolute number of breeders, but on the ratio of female to male breeders [3]. A population with a high number of female breeders but hardly any male breeders won't produce as many eggs as a population with moderate numbers of both.

To derive the new fecundity terms, we start with the harmonic mean *marriage function* $B \equiv B(X_i, X_m, Y_m)$ given by

$$B(X_i, X_m, Y_m) = \frac{2Y_m(X_i + X_m)}{Y_m + X_i + X_m},$$

which gives the number of matings as a function of breeding males and females. This choice of marriage function represents the harmonic mean of $X_i + X_m$ and Y_m and is believed to be the most biologically accurate representation of the number of matings as a function of males and females [3]. Some of the important properties of this function that are inherited from the properties of the harmonic mean include:

1. $B = X_i + X_m = Y_m$ when $X_i + X_m = Y_m$
2. $B \leq \max(X_i + X_m, Y_m)$
3. $\lim_{Y_m \rightarrow 0} B = 0$
4. $\lim_{X_i + X_m \rightarrow 0} B = 0$.

These properties are illustrated in Figure 2.2. In this figure, a total of 300 breeders is assumed. The number of male breeders is shown on the x-axis, and the number of female breeders is 300 minus the number of male breeders. $B = 150$ when $X_i + X_m = Y_m = 150$ (Property 1), $B \leq \max(X_i + X_m, Y_m)$ (Property 2), and lastly, $\lim_{Y_m \rightarrow 0} B = 0$ and $\lim_{X_i + X_m \rightarrow 0} B = 0$ (Properties 3 and 4).

Assuming male breeders have no sexual preference for one female breeder stage class over the other, the fraction of matings coming from immature and mature

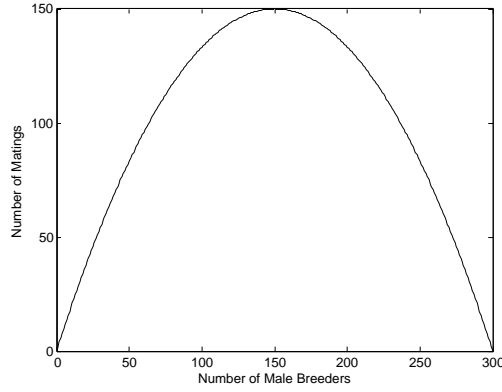


Figure 2.2: The effect of the number of male breeders in a terrapin population on the number of matings, assuming a total of 300 breeders.

females, denoted by B_{X_i} and B_{X_m} , respectively, are given by

$$\begin{aligned} B_{X_i} &\equiv \frac{X_i}{X_i + X_m} B = \frac{2Y_m X_i}{Y_m + X_i + X_m} \\ B_{X_m} &\equiv \frac{X_m}{X_i + X_m} B = \frac{2Y_m X_m}{Y_m + X_i + X_m}, \end{aligned} \quad (2.5)$$

so that $B = B_{X_i} + B_{X_m}$. This can be used to define the fecundities for the nonlinear model as

$$\begin{aligned} F_{X_i} &\equiv \frac{ku_i B_{X_i}}{X_i} = \frac{2ku_i Y_m}{Y_m + X_i + X_m} \\ F_{X_m} &\equiv \frac{ku_m B_{X_m}}{X_m} = \frac{2ku_m Y_m}{Y_m + X_i + X_m} \end{aligned} \quad (2.6)$$

which give the number of eggs produced per breeding immature and mature female, respectively. These fecundities are then substituted into (2.4) to arrive at the hatchling fecundity terms. Simulation of the nonlinear model is the same as the linear model, with the added step of updating the “fecundity” terms (2.4) in the matrix A in (2.2) at each time step.

Note that the linear model is equivalent to using a marriage function B that is *female dominant* [3], given by

$$B(X_i, X_m, Y_m) = X_i + X_m.$$

In this case, we can use (2.5) to show $B_{X_i} = X_i$ and $B_{X_m} = X_m$, as well as (2.6) to show $F_{X_i} \equiv ku_i B_{X_i}/X_i = ku_i$ and $F_{X_m} \equiv ku_m B_{X_m}/X_m = ku_m$. Thus, the linear and nonlinear models can be derived from the same equations with an appropriate choice of marriage function.

Using the appropriate marriage function for the linear and nonlinear models,

we can write the total number of eggs per year (*total birth*) as

$$X_i F_{X_i} + X_m F_{X_m} = k(u_i B_{X_i} + u_m B_{X_m}), \quad (2.7)$$

and the average number of eggs per mating pair per year (*average fecundity*) as

$$\frac{X_i F_{X_i} + X_m F_{X_m}}{B} = k u_i \left(\frac{B_{X_i}}{B_{X_i} + B_{X_m}} \right) + k u_m \left(\frac{B_{X_m}}{B_{X_i} + B_{X_m}} \right). \quad (2.8)$$

Thus, the average fecundity gives an indication of the relative proportion of immature to mature breeders in the population as a weighted average of the number of eggs produced per year by the immature and mature breeders. A relatively high average fecundity (closer to 20 or 30 eggs per breeder) suggests a larger fraction of mature breeding females, and a lower average fecundity (closer to 10 eggs per breeder) suggests a larger fraction of immature breeding females.

2.3 Modeling Crab Potting and Road Mortality

We make the following assumptions on crab potting and road mortality:

- Both male and female hatchlings are too small to be affected by crab pots.
- Immature and mature breeding females are too large to be affected by crab pots.
- Male juveniles and breeders, as well as female juveniles, are affected equally by crab pots.
- Both immature and mature breeding females are the only stage classes affected by road mortality, as they are the only classes to cross roads to build nests.
- Immature breeding females are less affected by road mortality as they have fewer clutches per season ($u_i < u_m$).

Letting c and r denote the proportion killed by crab potting and roads, respectively, where $0 \leq c, r \leq 1$, we modify the survival terms as follows:

$$\hat{\sigma}_Z = \begin{cases} \max(\sigma_Z - c, 0), & \text{for } Z = X_j, Y_j, Y_m, \\ \max(\sigma_Z - (u_i/u_m)r, 0), & \text{for } Z = X_i, \\ \max(\sigma_Z - r, 0), & \text{for } Z = X_m. \end{cases} \quad (2.9)$$

Whenever new values σ_Z for the survival terms are used, an iterative technique must be performed to calculate the other parameters in the system, as the growth

terms γ_Z in (2.1) depend implicitly on the unknown population growth rate λ . To illustrate, first initialize the sequence $\lambda^{(n)}$ such that $\lambda^{(0)} = \lambda_0$. This initial value λ_0 could for example correspond to some previous growth rate before an incremental change in σ_Z occurred. Now repeat the following until $\lambda^{(n)}$ has converged:

1. Update γ_Z using equation (2.1) with σ_Z and $\lambda^{(n)}$.
2. Update P_Z and G_Z using equation (2.3) with σ_Z and the updated γ_Z from Step 1.
3. Calculate $\lambda^{(n+1)}$ from (2.2) with the updated P_Z and G_Z from Step 2.

After convergence in N steps, set $\lambda = \lambda^{(N)}$. Linearization at the origin is ill-defined for the nonlinear model, and so to calculate the population growth rate (and stable stage distribution) in Step 3, we iterate the model until the stage distribution and growth rate stabilizes (which is guaranteed to occur since the model is frequency dependent [15, 16, 17]).

Chapter 3

Rhode Island Population

A little over ten years ago, Mitro [13] studied the one known population of diamondback terrapins in the state of Rhode Island. He used a linear model to examine the causes and rate of population growth. We use data given in Mitro's paper to calculate parameters applicable to our models (Table 3.1 and Table 3.2) and explore the behavior of the population using both the linear and nonlinear model.

We adjusted the hatchling survival rates and number of clutches per year for the mature breeders so that the population growth rate is $\lambda = 1.034$ and the average fecundity (see (2.8)) is equal to 19.0706 eggs per female [13]. Our hatchling survival $\sigma_{X_h} = \sigma_{Y_h} = 0.5545$ for the linear model is slightly different than that reported in [13] ($\sigma = 0.565$). This difference is slight, however, with the population growth rate and stable stage distributions a very close match.

3.1 Results

In the stable Rhode Island population with a growth rate of $\lambda = 1.034$, the distribution of terrapins in the linear and nonlinear models is very similar (Fig. 3.1), and matches closely the stable age distribution in [13]. The plurality of the population falls in the male breeder stage, and the size of the female mature breeder stage is also fairly large, as these final stages accumulate terrapins that remain there for the rest of their lives. The hatchling stages also contain a high proportion of the individuals, but then the proportion declines throughout the intermediate stages as mortality takes its toll.

Parameter	Linear	Nonlinear
P_{X_h}	0.3609	0.3497
P_{X_j}	0.7879	0.7879
P_{X_i}	0.7392	0.7392
P_{X_m}	0.9371	0.9371
P_{Y_h}	0.3609	0.3497
P_{Y_j}	0.4935	0.4935
P_{Y_m}	0.9405	0.9405
G_{X_h}	0.1935	0.1787
G_{X_j}	0.1561	0.1561
G_{X_i}	0.2048	0.2048
G_{Y_h}	0.1935	0.1787
G_{Y_j}	0.4505	0.4505
\tilde{F}_{X_i}	0.2722	–
\tilde{F}_{X_m}	0.6360	–

Table 3.1: Calculated persistence P and growth G parameters from (2.3), and constant “fecundity” terms from (2.4) used in the models (2.2).

Parameter	Value	Source
λ	1.034	[13]
$\sigma_{X_h}, \sigma_{Y_h}$ (linear)	0.5545	Calculated
$\sigma_{X_h}, \sigma_{Y_h}$ (nonlinear)	0.528371	Calculated
$\sigma_Z, Z \neq X_h, Y_h$	0.944	[13]
σ_e	0.097	[13]
h	0.8735	[13]
u_i	1	Assumed
u_m (linear)	2.3362	Calculated
u_m (nonlinear)	2.33625	Calculated
k	10	[20]
l	40	[13]

Table 3.2: Table of parameters used for the linear and nonlinear models.

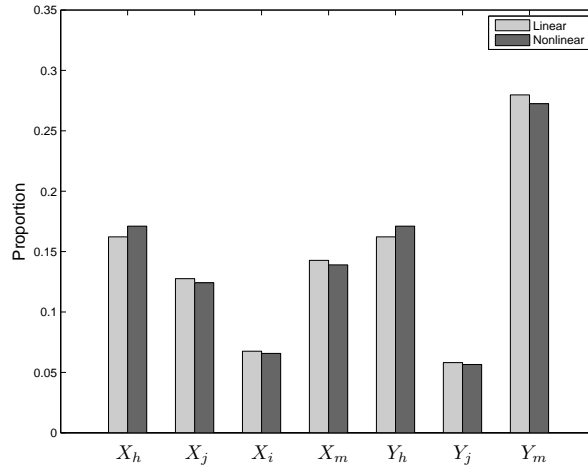


Figure 3.1: The stable stage distribution for both the linear and nonlinear models.

3.1.1 Crab Potting and Road Mortality Simulations

Figure 3.2 shows the change in the population growth rate (λ) as a function of the crab potting (left) and road mortalities (right). In the nonlinear model, the point at which the terrapin population begins to experience decline due to crab potting happens at a level of mortality of the affected stages of 6.6%. In the linear model, this tipping point does not occur until 11.6% mortality (close to 12% found in [1]). These results illustrate the benefit of using a nonlinear model, as it is more sensitive to changes that affect male portions of the population. The linear model has no way to account for the decrease in the number of males or the decrease in the male contribution to fecundity. As the adult males are killed off, only the nonlinear model reflects the resulting decline in egg number due to the shortage of breeding males. Note that a modification to the linear model was performed in [1] to account for a female:male sex ratio of 10:1, giving a critical point of crab potting at 9%.

Road mortality does not have as detrimental an effect on the growth of the population (Fig. 3.2). The linear model predicts a shift from population growth to decline at a lower level of mortality (7.6% of mature female breeders and 3.3% of immature female breeders) than does the nonlinear model (10.6% of mature female breeders and 4.5% of immature female breeders). The values for the two models are fairly close together, as both models are taking female survival into account. These results are supported by the findings of Gibbs and Steen (2005), who saw that the female to male ratio of terrapins decreases in areas with more roads [8]. In [1], the critical point for road mortality was found to be approximately 10% for immature and mature female breeders.

The ratio of female breeders to male breeders is greatly affected by both crab

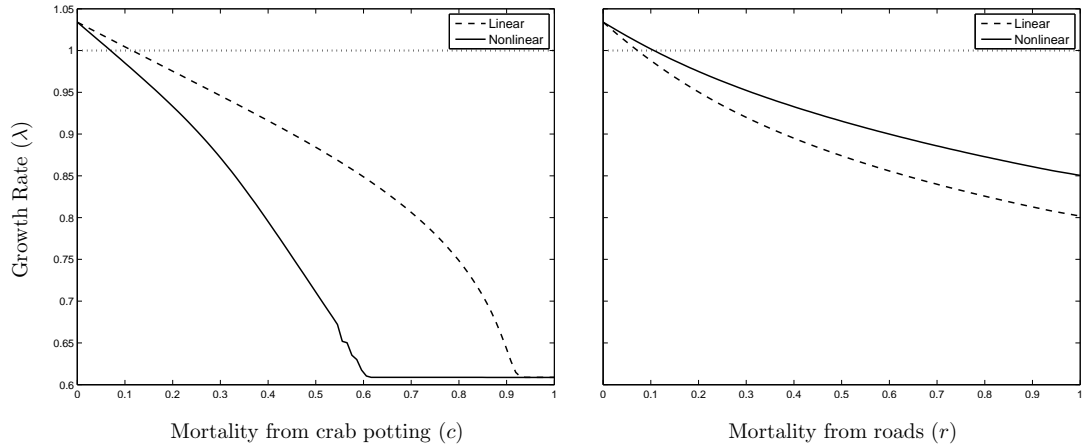


Figure 3.2: Population growth rate λ as a function of both crab potting c (left plot) and road mortality r (right plot) for both the linear (dashed line) and nonlinear (solid line) models. Dotted line denotes $\lambda = 1$, the critical value separating growth and decline. Critical point for crab potting: $c = 0.116$ (linear) and $c = 0.066$ (nonlinear). Critical point for road mortality: $r = 0.076$ (linear) and $r = 0.106$ (nonlinear).

potting mortality and road mortality (Fig. 3.3). As the amount of mortality from crab potting increases, so does this ratio. The increase occurs much faster under the nonlinear model, as it directly addresses male mortality, as discussed above. The rate of decrease in the ratio of female to male breeders due to road mortality is similar in both the models, although the linear model appears to be slightly more sensitive to the effects of such mortality.

The average fecundity, or number of eggs produced per breeding pair per year (see (2.8)), of terrapin populations that experience crab potting is actually higher than that of populations free from the negative influences of crab potting (Fig. 3.4). The decline in the size of the juvenile female stage caused by crab potting in turn diminishes the size of the immature breeding female stage. Those terrapins that survive to the mature breeding female stage begin to accumulate, as they are safe from the crab pots. These mature breeders produce greater numbers of eggs than the immature breeders, and do so for the remainder of their potentially long lives. This accounts for the increase in average fecundity that approaches $ku_m \approx 23.3625$, or the number of eggs produced per mature breeding female per year. However, the total birth, or total number of eggs produced per year (see (2.7)), declines at high levels of crab potting in the nonlinear model, as the total number of breeders is declining. This decline in the birth term does not happen to a great extent in the linear model, as it doesn't include male stages, as discussed above.

Both the average fecundity and the birth term decline as the level of road

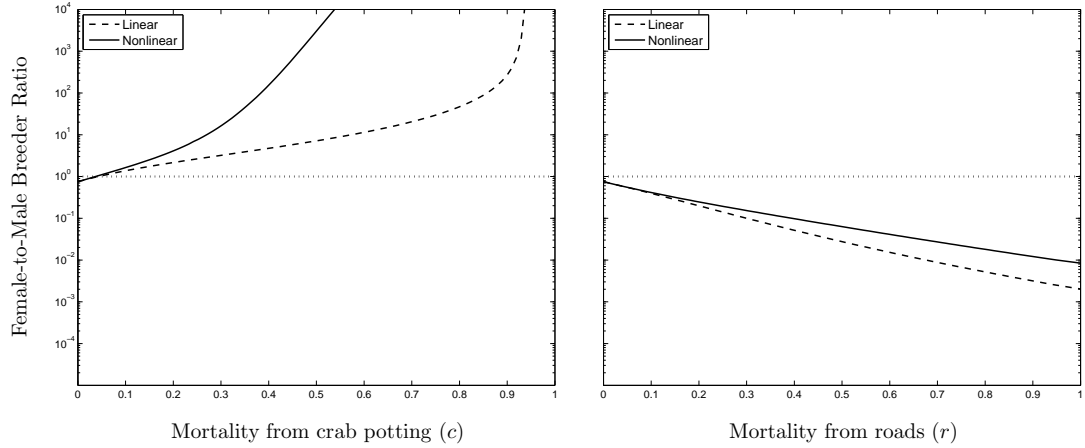


Figure 3.3: Female-to-male ratio of breeders as a function of crab potting c (left plot) and road mortality r (right plot) for both the linear (dashed line) and nonlinear (solid line) models. Dotted line denotes a ratio of 1, representing equal proportions of males and females.

mortality increases (Fig. 3.4). The fecundity approaches $ku_i = 10$, or the number of eggs produced per immature breeding female per year. This happens because road mortality disproportionately affects mature breeding females. The birth term for both models approaches 0 as road mortality increases, since in both models a complete lack of females results in no new hatchlings.

3.1.2 Egg Survival Simulations

We also examined the effects of egg survival on the Rhode Island population to determine the value of conservation measures aimed at nests. The egg survival obtained from [13] had a value of 0.097. As this value is increased, the values of crab potting and road mortality at which the population begins to decline also increase (Fig. 3.5). For instance, when the egg survival is doubled to 0.194 and road mortality is non-existent, the value of c at which $\lambda = 1$ roughly doubles. With that value for egg survival and no crab potting, the value of r at which $\lambda = 1$ more than doubles. The line along which $\lambda = 1$ shifts even farther when the original value for egg survival is quadrupled.

Egg survival does play a definite role in determining the rate of population growth, but it is much easier to reduce the rate of population decline by cutting down on the number of terrapins that drown in crab pots. As can be seen in Figure 3.5, increases in crab pot mortality more rapidly lead to smaller values of λ than increases in road mortality. Although compliance and enforcement issues may limit the effectiveness of BRD regulations, it is much less time consuming and costly to

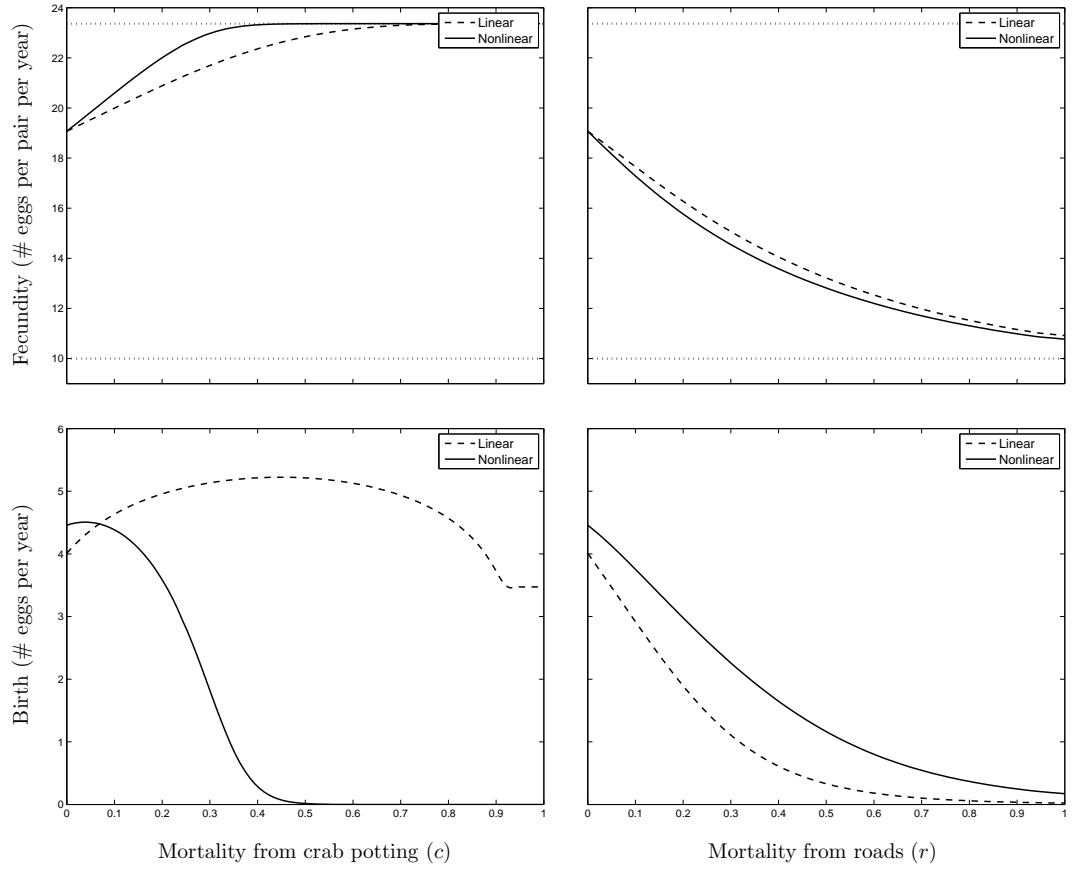


Figure 3.4: Average fecundity (2.8) (top) and total birth (2.7) (bottom) as a function of both crab potting c (left) and road mortality r (right). For fecundity, the dotted lines denote the fecundities for populations whose female breeders are either all immature (lower value) or all mature (upper value).

affix BRDs to crab pots than it is to protect nests full of eggs on beaches from threats such as predation by raccoons and erosion by storm surges [2].

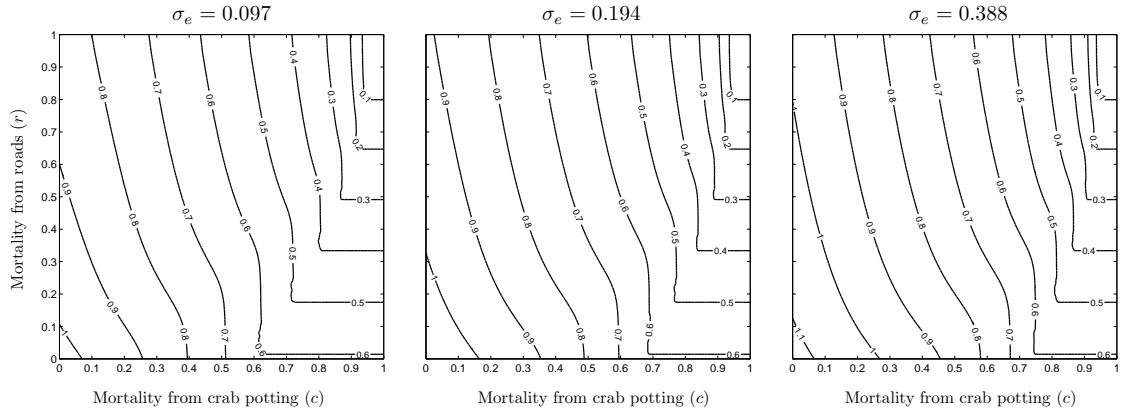


Figure 3.5: Population growth λ in the nonlinear model versus both crab potting c and road mortality r for three levels of egg survivorship: $\sigma_e = 0.097$ (baseline), 0.194 (double baseline) and 0.388 (quadruple baseline).

Chapter 4

Field Work: Local Populations

4.1 York County: Queen’s Creek

Multiple diamondback terrapin populations can be found near Williamsburg, Virginia (R. Chambers, College of William and Mary, pers. comm.). During the summer of 2013, we obtained a count of the terrapins present in a section of Queen’s Creek (37.298781, -76.662867) in York County, Virginia. This site is a 15 minute drive from the College of William and Mary’s main campus. We launched our canoe from a dock belonging to Patrick Owens, who kindly allowed us access to his property for the summer.

On 11 June we placed ten crab pots at various points along the more northern side of Queen’s Creek (the opposite side from the houses that bordered the creek) (Fig. 4.1). These pots were modified to include a “chimney” that allowed the trapped terrapins to come to the surface for air without escaping (Fig. 4.2). We checked the contents of each of the traps Monday through Friday beginning that week and concluding on 12 July. As with recreational and commercial crab pots, ours were only catching juvenile and male adult terrapins [18]. We recorded the sex, shell height, carapace (dorsal shell) length, and the trap number of each terrapin. We also recorded their age, which can be determined by counting the number of growth rings present on each scute (section) of their shell. Each year a new growth ring forms as the terrapin grows faster during the summer than the winter. Unfortunately, as a terrapin ages the growth rings become impossible to distinguish, as there are many rings and the shell becomes nearly worn down over time [2].

Before releasing them back into the creek, we used a triangular file to notch their shells with a binary system for identification in the event of a recapture. On Fridays we opened the traps so that any terrapins that swam in would be able to swim right back out. On Mondays we closed this opening and began the process



Figure 4.1: Queen's Creek in York, VA. Approximate crab pot locations designated by red dots. Map from www.google.com/maps.

again.

We captured a total of 47 individual terrapins: 9 female juveniles, 22 male juveniles, and 14 male breeders. Of the remaining 2, we neglected to determine the age of one, and the other escaped over the side of the boat before we could age it. Both were male. There were also 40 recapture events: 11 for female juveniles, 20 for male juveniles, and 9 for male breeders. As we expected, there were no hatchlings or female breeders present in the traps, as they are generally excluded from crab pots [18]. The results are displayed in Table 4.1.

We used the Schnabel Method to obtain an estimate for the size of the total population that can be caught in crab pots. The estimated number of terrapins is given by

$$N = \frac{\sum_{e=1}^n C_e M_e}{\sum_{e=1}^n R_e} \quad (4.1)$$

where C_e is the number of terrapins captured on day e , M_e is the number of previously caught terrapins in the creek on day e , and R_e is the number of recaptures on day e [21].

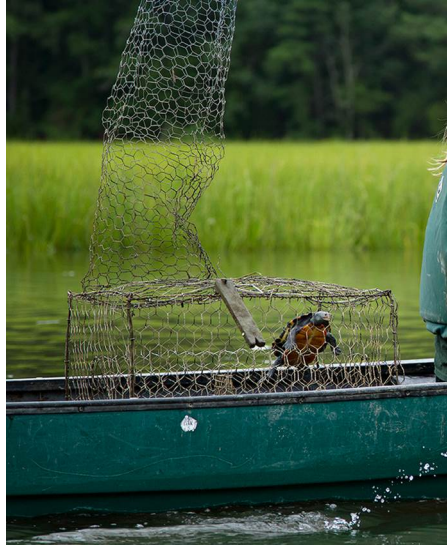


Figure 4.2: A crab pot modified by the addition of a chimney. Photo by Wendy Nelson (<http://vawendy.smugmug.com/Other/Terrapins>).

Stage Class	# Caught		Recaptures		Carapace Length (cm)	
	Q	M	Q	M	Q	M
X_h	0	0	0	0	n/a	n/a
X_j	9	47	11	8	10.7 – 17.7	8.9 – 16.7
X_i	0	20	0	1	n/a	10.2 – 17.0
X_m	0	0	0	0	n/a	n/a
Y_h	0	0	0	0	n/a	n/a
Y_j	22	8	20	0	10.2 – 13.6	9.0 – 11.4
Y_m	14	38	9	8	10.9 – 13.5	9.0 – 11.7

Table 4.1: Data gathered at Queen's Creek ("Q" columns) and Mud Narrows ("M" columns) during the summer of 2013.

For the terrapin data from Queen's Creek, we obtained an estimate of 55.9 for the total population size. This implies that we caught 84.07% of the population in our crab pots. We also applied the Schnabel Method to the data for each of the individual stage classes. We found that there were an estimated 9.36 female juveniles, 26.71 male juveniles, and 18.33 male breeders. These don't exactly add up to the estimate for the total population size, which included those terrapins whose age we failed to determine. The results suggest that the sex ratio of the juvenile stage classes is skewed strongly toward males, whose juvenile stage class lasts only two years, as opposed to the five years of the female juvenile stage classes. If this is indeed correct, it is possible that the sex ratio of the hatchlings is also weighted toward the males. However, data from additional years would be needed in order to more conclusively determine if the results obtained during the summer of 2013 are representative of the actual population present in the creek.

4.2 Accomack County: Assawoman Creek

During the summer of 2013, terrapin sampling was also being conducted on the Eastern Shore of Virginia by Scott Belfit, an Eastern Shore resident collecting data for a research project under the direction of Dr. Randy Chambers at the College of William and Mary. At different points during the sampling period (30 May to 2 August) there were anywhere from 4 to 14 modified crab pots placed in the Mud Narrows (37.829801, -75.516410) portion of Assawoman Creek located in Accomack County, Virginia. A total of 161 individuals were found in the traps. 47 were recorded as female juveniles, 20 as female immature breeders, 8 as male juveniles, and 38 as male breeders (Table 4.1). The ages of the remaining terrapins could not be determined. There were also 28 recapture events: 8 juvenile females, 1 immature breeding female, and 8 male breeders (S. Belfit, pers. comm.).

The Schnabel method was performed on these results as well [21]. The total estimated population size is 523.1 (including the individuals whose age could not be determined), with an estimated female juvenile stage class of 155.375, immature female breeder stage class of 199, and male breeder stage class of 103.5. The Schnabel Method could not be applied to the male juvenile stage class due to the lack of recaptures.

The results from this site were dramatically different than those obtained from the Queen's Creek data. Far more terrapins were caught in Mud Narrows than Queen's Creek. Additionally, the proportion of the sampled population made up of juvenile males was much higher in the Queen's Creek population. Breeding females were caught at Mud Narrows, unlike Queen's Creek. However, all of these were young breeders in the immature breeder stage class, ranging in age from 8 to

10.

4.2.1 Bycatch Reduction Devices

From 4 June until the conclusion of the field work on 2 August, 4 out of the 8 modified crab pots placed in Mud Narrows were fitted with BRDs. None of these pots caught any terrapins until the final day of sampling, when a single male terrapin of unknown age was captured. The effect of the BRDs on catch of crabs was not examined.

If the crab pots that were used that summer had been for commercial or recreational use and had not been modified, 161 diamondback terrapins (about 30% of the estimated population size) would likely have drowned. The results of the traps with the BRDs suggest that in bodies of water such as Mud Narrows that have a high abundance of terrapins, BRDs would have a significant impact on survivability and population growth.

Chapter 5

Conclusion

5.1 Future Work

5.1.1 Local Studies

Efforts to model the Queen's Creek and Mud Narrows populations, as well as other local populations, would benefit from continued field work in order to get a more accurate estimation of population size and growth. Over a period of multiple summers, enough information could be gathered to provide a set of data as comprehensive as that used in [13]. This would allow us to run the same simulations as we did for the Rhode Island population, painting a clearer picture of the effects of various human influences and other factors on these local populations.

A different capture method should be used on the terrapins for these longer term studies. We used the crab pots because they were readily available and easy to place, maintain, and check. A net, however, would have allowed us to capture the three stage classes we were already catching in the crab pots, plus the female breeder stage classes, which were excluded from the crab pots due to their large size [7]. While there would likely be more bycatch in nets, the sample of terrapins captured would more accurately represent the makeup of the population.

Another option would be using crab pots with larger openings. During the last week of field work for the summer of 2013, we experimented with this by using wire cutters to widen two out of the four openings on half of the crab pots we had in Queen's Creek. The results we obtained during this week were not included in the data we present above. This option is likely not as effective as a net would be, because the altered openings might allow some of the juveniles and male adults to escape. However, during this week we did catch 3 female breeders. They were too old to determine exact age, but by their large size (carapace length from 19.6cm to 21.5cm and height from 7.8cm to 9.1cm) it was apparent that they would not

have fit into the crab pots with the original openings.

5.1.2 Modeling

Future mathematical research could focus on altering the model to add detail to the nonlinear fecundity terms. The addition of a term for the size of a harem (the number of females one male will mate with) could be included. According to [10], a harem size of five females yields 80% to 90% fertility in a captive population. If this is also the case for terrapin populations in the wild, certain levels of crab potting would actually increase the fecundity of the population, if it pushed the ratio of females:males closer to 5:1. Also, a parameter for the proportion of eggs that are female (or male) could be included, as terrapin eggs undergo temperature-dependent sex determination (TSD) [2]. Temperatures of at least 31° C (87.8° F) lead to female hatchlings, while temperatures of less than 27° C (60.6° F) lead to male hatchlings [11].

Other directions for future research could include examining demographic stochasticity, as well as the sensitivities and elasticities of the various parameters in the nonlinear model. As in the loggerhead turtle study [6], a sensitivity analysis would more conclusively determine how the population would respond to changes in survivability across different stages, as well as changes in crab potting and road mortality. Terrapin conservation efforts would benefit from the knowledge of exactly how responsive each stage class is to boosts or declines in survival, as they would be able to allocate their resources and funds accordingly to counteract effects of human influences on terrapin populations.

5.2 Conclusions

As we have not validated the linear and nonlinear models against actual population data, we cannot conclusively determine which better predicts the behavior of terrapin populations. We would need a population that has been studied over multiple years (as in [13]), that we know to have been affected by a certain degree of crab potting and road mortality, in order to see which model better represents the dynamics that are occurring. The importance of collecting data for model validation is strengthened by the different level of importance each model attributes to crab potting versus road mortality: critical values for population decline are nearly opposite in each case ($c = 6.5\%$, $r = 10.6\%$ for the nonlinear model; $c = 11.6\%$, $r = 7.6\%$ for the linear model). However, the nonlinear model has the potential to be a more accurate depiction of the dynamics, as it takes the male contribution to fecundity into account. This could be especially important in populations that experience

crab potting.

Diamondback terrapin populations can benefit from measures to protect the terrapins from both crab pot and road mortalities. The modeled Rhode Island population was growing, but at a slow rate ($\lambda = 1.034$) [13], and both models suggest that a relatively small push could send it into decline. Crab potting is theoretically an easier problem to fix, which the nonlinear model suggests would have a larger effect on an affected population. Unfortunately, there can be much resistance to the use of BRDs, as they are viewed as potentially harmful to the crabbing industry (R. Chambers, College of William and Mary, pers. comm.). Educating both recreational and commercial crabbers about the benefits of BRDs could have a positive effect on the terrapin population.

A study performed in Georgia in an area with low levels of road traffic found that road mortalities did not contribute to population decline [9]. This illustrates the importance of tailoring conservation efforts to the specific locations where they will be applied. It would be more effective to focus on promoting the use of BRDs in the marsh around this Georgia population. But in highly developed areas with frequently used roads, it could be more effective to look into a long-term management plan to reduce road mortality.

We suspect that the local terrapin populations could be experiencing significant pressures due to crab potting. Road mortality is less likely to be an issue, as roads typically run alongside marshes as opposed to cutting through them (R. Chambers, College of William and Mary, pers. comm.). However, speculating as to the long term effects of these human linked influences are all we can do at the moment, until more data are available on which to base a conclusion.

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